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Holocene variation in the small mammal fauna of central Chile

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The species composition of contemporary communities is a recent phenomenon emerging from the individualistic response of each species to changing environmental conditions (Gleason 1926). Changes in species composition varies at different time and spatial scales. Therefore, understanding of contemporary communities requires to place the local community in its historical and biogeographical context (Ricklefs and Schlutter 1993).

Contemporary small mammal assemblages have fewer species than those of recent past. Chilean caviomorph assemblages are depauperated and nested subsets of past faunas (Simonetti 1994). Local extinctions during the Holocene determined that current distributional ranges were attained recently, following a more widespread distribution of several taxa (Saavedra et al. 1991; Simonetti and Saavedra 1994). The early Holocene caviomorph assemblages of the Andes of central Chile comprised six species, two becoming locally extinct around 1,500 years BP. Nevertheless, the generality of the Holocene reduction in species richness in central Chile needs to be established. Here, we further analyze the late Holocene dynamics of caviomorph assemblages in the Coastal Range of central Chile, and compare it to that of the Andean range (Simonetti 1994). If species impoverishment is a general event, past assemblages at the Coastal Range ought to be richer than current ones, following a similar trend of species depauperation than in the Andes. Furthermore, we will examine whether changes occurred simultaneously or if they vary geographically.

New samples of the Coastal Range come from prehistoric rodent assemblages recovered in three archaeological sites located in Las Chilcas (Las Chilcas 1: 32°53′ S, 70°49′ W, Las Chilcas 2: 32°51′ S, 70°52′ W, and Piedra del Indio: 32°54′ S, 70°48′ W, Fig. 1). These sites are small rockshelters, were humans and owls deposited small mammal remains among other biological and cultural material (Saavedra 1997; see Hermosilla 1997; Hermosilla et al. 1997a for excavation and recovery details). Species were considered attributes of the sample, considering only their presence-absence pattern (Grayson 1984). Past assemblages from Las Chilcas area were compared to present day ones as well as past assemblages from El Manzano basin (34°34′ S, 70°24′ W). Contemporary species composition for an area of 4 km around rockshelters was assessed from literature records, live trapping around rockshelters, sightings, and from prey remains of local predators (the owls *Tyto alba* (Scopoli, 1769) and *Bubo virginianus* (Gmelin, 1788) and the fox *Pseudalopex* sp.).

A total of 21,459 bone specimens of small mammals was recovered. However, only 4,164 were identifiable to the family level. From these, 2,619 (63%) were from four caviomorph species: *Abrocoma bennetti* Waterhouse, 1837, *Octodon bridgesi* Waterhouse, 1895, *Octodon degus* (Molina, 1782), and *Spalacopus cyanus* (Molina, 1782) (Tab. 1). Las Chil-

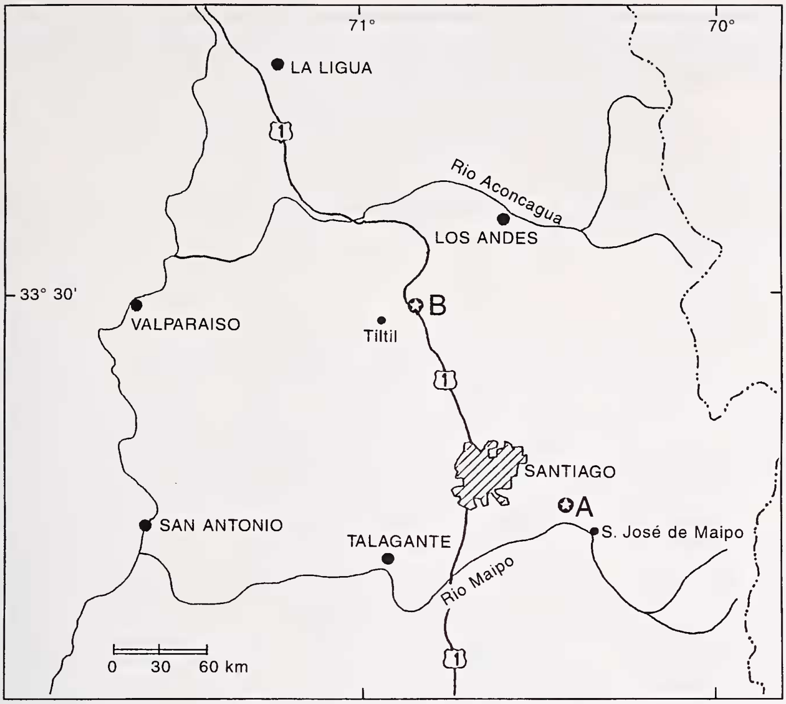

Fig. 1. Locations of sites sampled. The three rockshelters of Las Chilcas area are shown together (B) as well as the two rockshelters at El Manzano basin (A).

cas 1 rockshelter yielded a sequence of 2,800 years. A total of 1,206 caviomorph specimens was recovered from the four caviomorph species (Tab. 1). Other species recovered were *Abrothrix* sp., *Oligoryzomys longicaudatus* (Bennet, 1832), and *Phyllotis darwini* (Waterhouse, 1837), all myomorphs. They were not included in our analysis due to their low sample size (combined NISP = 129). At Las Chilcas 2, a sequence of at least 2,000 years was established. Here, 633 specimens of the same four caviomorph species were retrieved (Tab. 1), together with remains of *P. darwini* and unidentified cricetids (NISP = 75), that were excluded from our analysis. At Piedra del Indio, the sequence embraces at least 1,200 years, with 780 caviomorph remains recovered (Tab. 1) together with *O. longicaudatus* and *P. darwini* (combined NISP = 34), also excluded from the present analysis.

The three sites shared four caviomorph species, being present from 2,800 to 160 years BP. Only one species, *O. bridgesi* disappeared, around 160 years BP (Tab. 1). Currently, this species does not inhabit the area, as assessed by published records (Redford and Eisenberg 1992), live trapping and predator diets. Only *A. bennetti*, *O. degus*, and *S. cyanus* have been recorded in the area. Comparing the same period of time, from 2,500 years ago onward, the fauna of Las Chilcas holds fewer species compared with El Manzano basin, where *Aconaemys fuscus* and *Lagidium viscacia* were present at different times (Tab. 1, Simonetti and Saavedra 1994; Simonetti 1994). *Aconaemys fuscus* disappeared from El Manzano only in recent times, and is now distributed in Chile between 35° and 40° S (Contreras et al. 1987), two degrees south of their past distribution. *Octodon bridgesi*, an habitat specialist, persisted up to 160 years BP in Las Chilcas, but at El Manzano basin it disappeared by 1,500 years BP (Tab. 1; Simonetti and Saavedra 1994; Simonetti 1994).

Table 1. Species composition of caviomorph assemblages from the coastal range (Las Chilcas 1, Las Chilcas 2, and Piedra del Indio) and the Andean range (El Manzano 1 and La Batea 1, from Simonetti 1994) of central Chile. Abbreviations: *Aben*, *Abrocoma bennetti*; *Afus*, *Aconaemys fuscus*; *Obri*, *Octodon bridgesi*; *Odeg*, *O. degus*, *Scya*, *Spalacopus cyanus* and *Lvis*, *Lagidium viscacia*. nisp is the number of identified specimens.

SITE/STRATUM OR DATE (years B.P.)	*Aben*	*Afus*	*Obri*	*Odeg*	*Scya*	*Lvis*
Las Chilcas 1						
Present	•			•	•	
700	•		•	•	•	
1,420–1,820	•		•	•	•	
1,970	•		•	•	•	
2,790				•	•	
Total nisp	197		6	775	228	
Las Chilcas 2						
Present	•			•	•	
36–160	•		•	•	•	
undated	•		•	•	•	
2,020	•			•	•	
Total nisp	267		3	355	8	
Piedra del Indio						
Present	•			•	•	
undated	•		•	•	•	
1,240	•			•	•	
Total nisp	45		3	613	119	
El Manzano 1						
Present	•			•	•	•
1,500	•	•		•	•	
undated	•	•	•	•	•	•
undated	•		•	•	•	•
8,900	•	•	•	•	•	•
undated	•	•	•	•	•	
Total nisp	12	14	24	66	99	6
La Batea 1						
Present	•			•	•	•
undated	•	•		•	•	•
1,500	•	•		•	•	•
2,400	•	•	•	•	•	•
4,500	•	•	•	•	•	•
undated	•	•		•	•	•
5,600	•	•		•	•	•
undated	•	•	•	•	•	•
Total nisp	118	44	16	203	359	11

The structure of current caviomorph assemblages in central Chile is a recent phenomenon, originating by a reduction in the number of species from Holocene assemblages, but the time at which current assemblages attained their modern structure varies geographically. While local extinctions shape the structure of modern assemblages, its occurrence is heterochronic. This difference could be due to a distinct prehistoric land-use regime. Central Chile was hetereogeneously used by prehistoric people, which could have triggered a mosaic of small mammal assemblages depending on the type and intensity of the land use (SIMONETTI and CORNEJO 1990; CORNEJO and SIMONETTI 1992).

The local extinction of *O. bridgesi* at El Manzano has been attributed to human disturbance of its habitat. This species inhabits only dense woodlands, which were cleared by prehistoric people to prepare landfields for horticulture. The disappearance of this species at El Manzano basin coincides with the settlement of horticulturists in the area, which was persistently used for over 9,000 years (SIMONETTI and CORNEJO 1990; CORNEJO and SIMONETTI 1992; SIMONETTI 1994). In contrast to El Manzano, Las Chilcas never supported a resident human population, being an area marginally used as a stopover while moving between adjacent basins or in an Andes-coast circuit (HERMOSILLA et al. 1997b); that is, under reduced human pressure, *O. bridgesi* persisted until modern times. Its more recent extinction could be associated to the increased use of the Coastal Range during the 18th and 19th centuries, when it was more intensively used as a source of fuel wood for mining as well as wheat production to supply Californian and Australian gold miners (ASCHMANN 1991). Wood cutting for mining and land clearing could have modified the dense habitat preferred by *O. bridgesi* as prehistoric settlers did in past times at El Manzano.

The heterogeneity in the timing of the faunal changes is related to differential patterns of prehistoric land use, generating a mosaic of impacts and assemblages across the space and time. To ignore the vicissitudes of this fauna may lead to equivocal interpretations about the discrepancies in convergent evolution in Mediterranean ecosystems. Regarding small mammals, central Chile is considered poor in species compared to California (GLANZ 1977). However, when extinct species are taken into account, differences are greatly reduced. Therefore, discrepancies are recent and the result of the long-term human intervention of the habitat (SIMONETTI 1994). Recently, a debate arose concerning the causes for the depauperate condition of small mammal fauna of central Chile. Based on cricetid species, isolation versus aridity is argued as the key factor shaping a species-poor fauna (CAVIEDES and IRIARTE 1989; MESERVE and KELT 1990). These claims ought to be re-evaluated as richer and more complex assemblages than previously known inhabited central Chile during the Holocene. Clearly, if the structure of modern assemblages is to be understood, both modern and past distributions must be known. Prehistoric land use has affected the local distribution of several taxa and the structure of assemblages from tropical, temperate and to Mediterranean regions (e. g. BLONDELL and VIGNE 1993), and Chile is not an exception. As for contemporary caviomorph assemblages, they not only are a recent biological phenomena but also reflect long-term human impact which are heterochronic at different localities in central Chile.

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